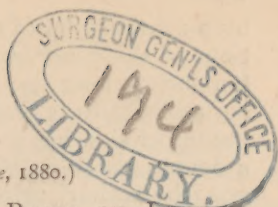


PACKARD (A.S.) Jr.

On the internal structure
of the brain of *Limulus polyphemus*



A. S. Packard Jr



(From the American Naturalist, June, 1880.)

ON THE INTERNAL STRUCTURE OF THE BRAIN OF *LIMULUS POLYPHEMUS*.¹—Several years ago I attempted to study the brain of the horse shoe crab (*Limulus polyphemus*), and had it sliced into a large number of sections. Owing to interruptions these sections, made from unstained alcoholic specimens, were not examined: during the past winter I have been able with the aid of Mr. N. N. Mason, of Providence, to take up the study afresh. Mr. Mason has kindly made sections, both transverse and horizontal, stained with osmic acid; also sections of the brain of the supra-oesophageal ganglion of the lobster, stained with picro-carminé, for comparison. The following results, then, are based on over two hundred sections of the supra-oesophageal ganglion of *Limulus*, but more especially on one brain, which was cut by Mr. Mason into fifty-six sections, from $\frac{1}{1000}$ to $\frac{1}{800}$ of an inch in thickness, and another cut into over forty. The examination of a few sections of the lobster's brain, enabled me to comprehend more readily the recent papers of Dietl, Newton and Krieger on the brain of the Decapodous Crustacea and of the insects, and thus give me a standard of comparison by which to study the topography and histology of the brain of *Limulus*.

General Anatomy of the Brain.—The singular relations of the central nervous system of the adult *Limulus*, have been fully described and beautifully illustrated by A. Milne Edwards, and Dr. Dohrn and myself have described its general anatomy in the larval stage. The central nervous system of *Limulus* consists of an oesophageal collar, mostly made up of six pairs of ganglia, from which nerves are distributed to the six pairs of foot-jaws (gnathopods), while the ring is closed or completed in front by the brain, or what corresponds to the supra-oesophageal ganglion of normal Crustacea and insects. In these Arthropoda, the brain is situated in the upper part of the head in a plane parallel to but quite removed from that of the rest of the ganglionic chain; in *Limulus*, however, the brain is situated directly in front of and on the same plane with the rest of the central nervous system. Milne Edwards states that the oesophageal ring, as well as the posterior part of the nervous system, is enveloped by an arterial coat; he also states that the brain and nerves are enveloped in a similar arterial coat, but this we have failed to find; the brain is protected by a thick membrane ("perineurium" of Krieger) formed of fibrous connective tissue, and the nerves are protected

¹Read at the meeting of the National Academy of Sciences, held at Washington, April 21, 1880. By A. S. Packard, Jr.

by a continuation of this membrane, as several longitudinal sections of these nerves have taught us. The brain in a *Limulus* ten inches long, exclusive of the caudal spine, is about five or six millimetres in diameter; it is flattened slightly above, and on the upper side has a shallow median furrow, indicating that it is a double ganglion. Three pairs of nerves and a median unpaired one (the ocellar), arise from the upper third of the anterior face of the brain. The two optic nerves are the largest ones, arising one on each side of the median furrow, so that the fifth to fifteenth sections made by the microtome, pass through them. Next below (from above downwards) is the origin of the ocellar nerve, which, as described by A. Milne Edwards, is single, arising from the median line; on each side and in nearly the same plane, arise two tegumental nerves, and directly below a second pair of larger nerves (fronto-inferior tegumental) descend vertically. No nerves arise from the lower half or two-thirds of the brain, which is smooth and rounded, with no median furrow underneath. It will thus be seen, that, as stated by A. Milne Edwards, there are no antennal nerves, such as exist as a rule in Arthropods except Arachnida. This we have proved in the same manner as Milne Edwards, by laying open the arterial coat or modified neurilemma, which reaches to the posterior end of the brain, and seeing that the fibres of the nerves sent to the first pair of legs originate quite independently of the brain itself.

Internal Structure and Histology of the Brain.—Transverse sections of the brain throw but little light on the topography, as the nerve fibres extend horizontally, the nerves being sent out horizontally and from the anterior end only of the brain; hence the examination of nearly two hundred sections threw little light on the topography, and considerable time was spent in a vain and baffling attempt at understanding the geography of this ganglion.

The study of two brains each sliced horizontally into about fifty sections, carefully mounted by Mr. Mason in consecutive order, finally enabled me to arrive at a tolerably complete idea of the relations of parts, so that I could mentally construct a model of the brain of *Limulus*, and compare it with the normal Arthropod brain.

The histological elements of the brain of *Limulus* are three in number. 1. Large ganglion cells, filled densely with granules and with a well-defined nucleus similarly filled and with a granular nucleolus. These cells may be crowded or loose, with the granules fewer in number, and with loose, thick cell-walls; they terminate in large fibres which sub-divide. 2. Similar cells, but smaller with less protoplasm, and like those in the lobster's brain. 3. Nerve fibres; these, like the large sized ganglion cells, from which they originate, are stained tawny yellowish-brown with osmic acid. These fibres are large, coarse, their granular contents very homogeneous, and they closely resemble the nerve fibres distributed to the compound and simple eyes. Certain fibres near the origin of the optic nerves, are distinctly nucleated

at intervals. 4. Rounded masses, consisting wholly of nuclei, enclosed in a network of fibres, which stain dark brown with osmic acid; these bodies form the larger part of the substance of the brain, while staining dark brown with osmic acid; in unstained alcoholic sections these masses are dark or grayish, the substance or fibres enclosing them, being whitish, by transmitted light. The brain is enveloped by a thick perineurium, formed of a fibrous tissue, and some (probably) elastic tissue, which occasionally penetrates into the brain-substance between the white rounded fungoid masses, forming the mesh-work surrounding them. The general topography of the brain of *Limulus* is on a simple plan compared with that of Decapodous Crustacea and insects. The brain is mostly composed of large irregular rounded masses or balls of nuclei, with a thick fungoid or ruffle-like periphery, formed by a layer of secondary smaller rounded granular masses. The center of the primary masses is stained paler brown by osmic acid. These masses are often seen in section, rounded, but more often are irregular, not closed spheroids; these fungoid or nucleogenous bodies extend through the brain like ruffles. The lower half or two-thirds of the entire brain is apparently filled with these nucleogenous bodies, as we may provisionally designate them. In the upper third of the brain, whence the nerves originate, the larger ganglionic cells and the nerve fibres appear, and preserve a definite topographical relation to the entire brain. The nucleogenous bodies are confined at the top to each side of the brain; the central and hinder regions are filled with the large ganglionic cells, mixed with numerous much smaller ones, and the mass of nerve fibres which spring from them, becomes larger from the upper third to the top of the brain where the optic fibres originate. Opposite the beginning of the optic nerves, these large nerve fibres are seen directed towards the origin of the nerves as if they were the roots, as they undoubtedly are. In the section passing through the ocellar nerve and the tegumentary nerves on each side, the fungoid masses are situated in the front of the brain; but they disappear from the front higher up at the origin of the optic nerves, and occupy a much more restricted area on the sides of the brain. Thus the tract of nerve fibres on either side of the brain is irregularly wedge-shaped, the apex situated near the centre of each hemisphere, and the base spreading out on the top, thus crowding to the outer walls the nucleogenous bodies.

It would thus appear as if the lower half of the brain were in an indifferent state,¹ and that the dynamic part were confined to the upper third, the region giving origin to the nerves of sensation.

¹ This area, made up of granules and nuclei, seems really to be connective tissue, and to represent the connective tissue in which the ganglia of the embryo of the young larva are embedded. There seems no reason why the brain should not be partly formed from connective tissue as much as the remaining ganglia, as we have seen them to be in different sections of different ganglia, all or nearly all except the supra-oesophageal one.

The asymmetry of the brain is remarkable; the large ganglionic cells are most abundant in the center behind the middle and from there to the posterior side of the brain; a median line is slightly indicated by the arrangement of the fungoid masses. The tract composed of large nerve fibres with scattered ganglionic cells on the left side is very much more extensive than on the right.

Comparison with the brain of other Arthropods.—So wholly unlike in its form, the want of antennal nerves, and internal structure, is the supra-oesophageal ganglion, or "brain," of *Limulus* to that of insects and the higher Crustacea, that it is very difficult to find any points of comparison.

Histologically, judging by my specimens of the brain of the lobster which are stained with carmine, the brain of *Limulus* agrees with that of other Arthropods in having similar large ganglion-cells; the smaller ganglion-cells, so abundant in the brains of insects and Crustacea, are ~~wanting~~ in *Limulus*. There are, in *Limulus*, no *ballen-substanz*-masses homologous with those of the other Arthropods nor any "mush-room" bodies.

Topographically the internal structure of the brain of *Limulus* is constructed on a wholly different type from that of any other Arthropodous type known, so much so that it seems useless to attempt to homologize the different regions in the two types of brain. The plan is simple in *Limulus*; much more complex in Arthropods, especially in the brain of the craw-fish, as worked out by Krieger, as in the Decapodous brain there arise two pairs of antennal nerves besides the optic pair, and in external form the two types of brain are entirely unlike. The symmetry of the brain of the crayfish, as of the lobster and insects, is marked throughout, each hemisphere exactly repeating in its internal topography, the structure of the opposite side; the symmetry of that of *Limulus* is obscure and imperfect.

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present



